

A PRELIMINARY RADIOTRACKING STUDY OF MOVEMENTS, ACTIVITY PATTERNS AND HABITAT USE OF FREE-RANGING GABOON VIPERS, *BITIS GABONICA*

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RÉSUMÉ

Les mouvements diurnes, les patrons d'activité, l'utilisation des macrohabitats et la sélection des substrats ont été étudiés par radiotélémétrie chez quatre vipères du Gabon (*Bitis gabonica*) adultes, deux mâles et deux femelles. L'étude a été conduite durant la saison sèche (suivi par radiopistage du 1^{er} au 20 mars 1998) dans le sud-est du Nigéria. Les émetteurs, pesant environ 4 g, ont été implantés dans l'animal. Les vipères radio-équipées restèrent longtemps inactives sous terre. Trois d'entre-elles ont montré une grande activité nocturne en milieu ouvert. Les quatre ont été très actives durant les premières heures du jour. Ces vipères ont évité les terres cultivées et ont affiché une préférence significative pour les chablis dans les parcelles de forêt sèche. Les domaines vitaux moyens, calculés par la méthode du polygone convexe minimum, furent de 1,6 ha pour les mâles et de 0,8 ha pour les femelles. Les distances moyennes parcourues chaque jour furent significativement plus grandes chez les mâles que chez les femelles. Pour les deux sexes, les distances moyennes parcourues quotidiennement furent significativement plus fortes de nuit que de jour. Des parades nuptiales, des accouplements et des affrontements sexuels entre mâles furent parfois observés durant la période d'étude. Les vipères ont parfois utilisé des termitières comme abris.

SUMMARY

Radiotelemetry was employed to study daily movements, activity patterns, macrohabitat use, and substratum selection of four Gaboon vipers (*Bitis gabonica*), two adult males and two adult females. The study was carried out during the dry season (1-20 March, 1998) in south-eastern Nigeria. Transmitters, weighing approximately 4 g, were internally implanted. Gaboon vipers spent considerable time inactive below-ground. There was considerable nocturnal activity in the open in three of four specimens, and considerable above-ground activity during the early morning hours in all the four radiotracked specimens. These vipers showed a significant preference for the clearings inside dryland rainforest patches, and avoided cultivated lands. Males used a wider spectrum of macrohabitats than females, these latter being confined almost exclusively to dry forest clearings. Home-ranges, calculated by minimum convex polygon method, averaged 1.6 ha in the males and 0.8 ha in the females.

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Average daily distances moved were significantly higher in males than in females. In both sexes, average daily distances moved were significantly higher during night hours than during daylight hours. Courtships, matings, and sexual combats between males were sometimes observed during the study period. These vipers used sometimes the termite nests as shelters.

INTRODUCTION

Radiotelemetry on wildlife began in the late 1950's, and permitted since then considerable advancement of the knowledge of ecology and life-history traits of a number of elusive organisms, from insects to sharks, and from crustaceans to whales (e.g. see Amlaner & MacDonald, 1980; Priede & Swift, 1992). Free-ranging populations of snakes have been intensively studied by radiotelemetry since the early 1970's (e.g. see Fitch & Shirer, 1971), and many aspects of their elusive behaviours have been clarified due to the appropriate use of such a method of remote animal monitoring (e.g. see Reinert, 1992). However, as a consequence of the relatively expensive nature of this technique materials (transmitters, receiver, etc), radiotelemetric studies on free-ranging snakes have been done almost exclusively in north America (e.g. Plummer & Congdon, 1994), Australia (e.g. Slip & Shine, 1988), and Europe (e.g. Madsen, 1984; Naulleau *et al.*, 1997), and not in the developing countries such as the ones of Africa (but see Bodbijl, 1994). Therefore, most of the snake species living in these developing countries are immensely less known than those living in the advanced countries of the northern hemisphere.

In this study we present data on daily movements, activity patterns, habitat use, and substratum preference of radiotracked Gaboon vipers (*Bitis gabonica*) from a rainforest area of south-eastern Nigeria. Ecological data on free-ranging Gaboon vipers are scarce (Luiselli & Akani, 1998; Luiselli *et al.*, 1998a, 1998b), and radiotelemetry has been just occasionally used earlier with this large-sized viperid species (Bodbijl, 1994). Thus, although based on only four specimens our telemetric data could provide the first detailed information on some aspects of the field ecology of this largely unknown tropical snake species.

MATERIALS AND METHODS

THE SPECIES

The Gaboon viper, up to 2 m long, is one of the largest and most venomous viperids of the world, and is characterized by a heavily built body with bizarre dorsal colour patterns which are superb camouflages in the forest litter (Phelps, 1989). It inhabits tropical forests of sub-Saharan Africa, from Guinea to southern Sudan in the north, through Uganda, western Kenya, Tanzania, Zambia, Zaire, to northern Angola and northern Zululand (Spawls & Branch, 1997). In Nigeria, it is found only in the southern forested regions (subspecies *gabonica*), where it feeds mainly upon small mammals (Luiselli *et al.* 1998b) and shows a clear seasonality in the reproductive timing, with mating occurring during the dry season, and births during the wet season (Luiselli & Akani, 1998; Luiselli *et al.*, 1998a).

STUDY AREA

The study was conducted during the dry season (February-March 1998) in the surroundings of Eket (Akwa-Ibom State, $04^{\circ} 50' \text{ N}$, $07^{\circ} 59' \text{ E}$), a locality of south-eastern Nigeria situated along the hydrographic basin of the Qua-Ibo (= Kwa-Ibo) River (Fig. 1). This area is important for the economy of Nigeria because of its big oil industry installations. The study area, 37.5 ha surface, was a patchy mosaic of dry rainforest (35 % of the whole surface), swamp-rainforest (20 %), cultivated land (cassava and oil palm, 35 %), and suburbia (10 %). Details of climate and environmental characteristics of the study area are presented elsewhere (Luiselli *et al.*, 1998b).

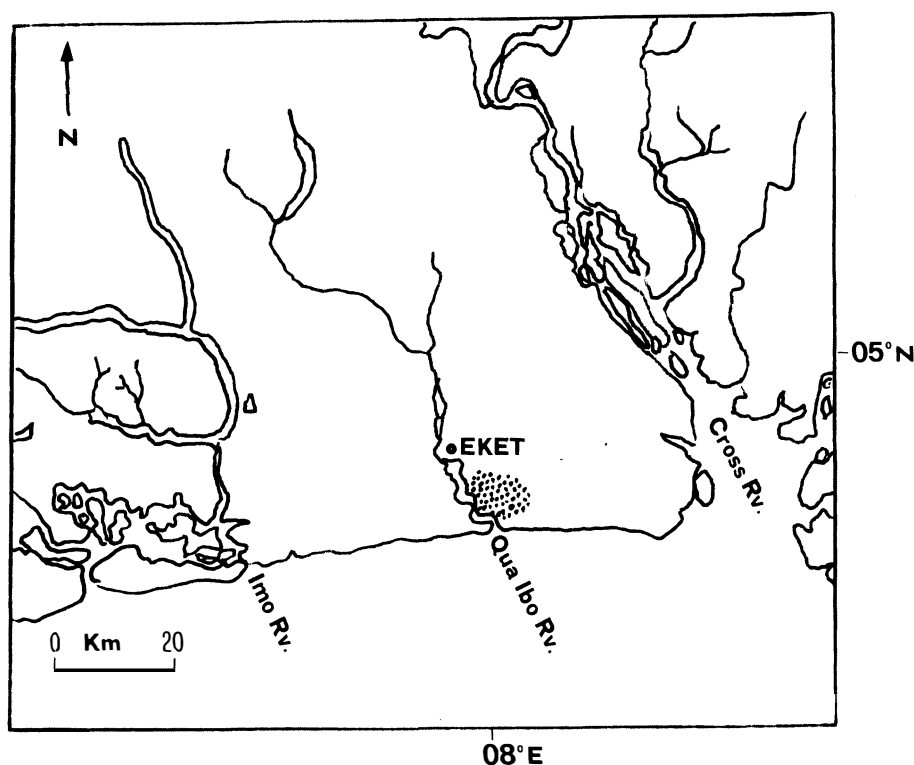


Figure 1. — Map of south-eastern Nigeria, showing the study area, situated in the surroundings of Eket, one of the main urban centres of Akwa-Ibom State.

METHODS

Four Gaboon vipers were captured by hands in the study area, anaesthetized, and equipped with implanted radiotransmitters. The radiotracked specimens were two males (specimen A = 118 cm total length; specimen B = 119 cm total length)

and two non-gravid females (specimen C = 127.5 cm total length; specimen D = 114.5 cm total length), which were returned to their original home ranges after radiotransmitter implantation.

The transmitters, encapsulated in polyethylene and abdominally implanted, weighed approximately 4 g (i.e. much less than 1 % of the weight of the snake carrying the transmitter, so they were very unlikely to have affected the snake's behaviour — cf. Shine & Lambeck, 1985). Transmitters operated within the 171 MHz frequency range. They were assembled by the radio technical group of "Amertex Oil & Gas Nigeria Ltd", by partial following of the suggestions of Kenward (1987). The transmitter implantation did not compromise the health condition of the radiotracked snakes throughout the whole study period. The receiver CUSTOM CE-12, connected to a 4-element Yagi antenna, received signals within 100-200 m range. Reliable reception range varied with the snake's depth, topography and vegetation thickness, and the above-mentioned range would have been considerably wider in open territory, e.g. in savannas (Angelici *et al.*, unpublished data).

Radio-implanted vipers were given with a period of recovery of respectively 13 days (specimens C and D), 15 days (specimens B), and 16 days (specimen A) before field observations were made. The experimental study consisted of twenty days of continued radio-monitoring for every specimen (1-20 March 1998). Field days were subdivided into eight three-hour-long intervals. Every day each snake was located once in each of these daily intervals for a total of 160 locations throughout the whole research period. All daily times followed Lagos time.

On each location, we determined (1) whether the snake was active above-ground or below-ground, (2) the type of macrohabitat, and (3) the type of activity. Given the relative sedentarity of these specimens, we did not miss any fixes throughout the monitoring period. Moreover, even if the snake could not be seen, its location could be determined within an area of 1 m².

Whenever a telemetered snake was located, its location was recorded for classification of the macrohabitat into one of the following categories: (i) thick dry forest, (ii) clearings of the dry forest, (iii) grassy area, (iv) swamp-forest, (v) cultivated land. For analysis of macrohabitat type preferences, both above- and below-ground active snake locations were used.

The behaviour of snakes sighted above-ground was categorized into one of five types: (i) engaged in locomotion, (ii) actively engaged in feeding, (iii) alone and coiled, (iv) alone and partially lying stretched out (i.e. possible ambushing for prey), and (v) engaged in social groups. These behavioural categories were decided by following Starin & Burghardt's (1992) observational protocol of *Python sebae*, and modifying it on the basis of our personal field experience with Gaboon vipers.

A numerical measure of the breadth of macrohabitat use of the various monitored individuals was obtained by applying a modified Simpson's (1949) index to the numerical percent data. The similarities between individuals in the frequency of utilization of the various macrohabitat type categories were estimated by using the symmetric equation of Pianka (1973), with values ranging from 0 (no similarity) to 1 (total similarity).

Each location was noted on a map of the study area. Movements were measured as straight line distances between successive location points on the map. Home ranges were calculated by determining the area of the minimum convex polygon including all locations of a given snake. Although (i) this method is surely

subjected to some potential bias, and (ii) it is likely to be more reliable for more prolonged monitoring times, nevertheless it allows comparisons with studies on other snake species (e.g. see Christian & Waldschmidt, 1984).

All data were analysed by SPSS (version for Windows) computer package, with all data being two-tailed and α set at 5 %.

RESULTS AND DISCUSSION

ABOVE-GROUND AND BELOW-GROUND ACTIVITY PATTERNS

Gaboon vipers of both sexes spent considerable amount of time hidden below-ground. This is shown by the fact that male A was below-ground on 44.4 % of the total number of locations ($n = 160$), male B on 45.6 %, female C on 70.6 %, and female D on 61.3 % (Table I). The two males were significantly more above-ground active than the two females (χ^2 with $df = 1$, $P < 0.0001$). The distribution of the fixes with above-ground active specimens (Table I) indicated that there was considerable nocturnal activity in specimens A, B, and D, and considerable above-ground activity during the early morning hours in all the four radiotracked specimens. Lowest levels of above-ground activity were detected between hr 1300 and hr 1559 in all the four monitored specimens. Specimens A, C, and D were very little above-ground active even between hr 1000 and hr 1259, but male B was often found in the open at that time (35 % of the total number of fixes). Above-ground activity peaked between hr 0700 and hr 0959 and between hr 1600 and hr 2159 in male A, between hr 0700 and hr 0959 and between hr 1900 and hr 2159 in male B, between hr 0400 and hr 0959 and between hr 1600 and 1859 in female C, and between hr 0700 and hr 0959 in female D.

In general we conclude that, despite some remarkable interindividual differences were noted (Mann-Whitney U test on the differences between individuals, $df = 3$, $P < 0.01$), above-ground activity of Gaboon vipers was concentrated in the relatively cool hours of the day, i.e. in the early morning and night hours (Table I). This pattern confirms on a quantitative basis previous data based on casual sightings of Nigerian specimens (Luiselli & Akani, 1998), but a tendency to avoid above-ground activity during the hottest hours of the day was also observed in conspecifics from southern Africa (Bodjil, 1994).

HABITAT USE

The frequency of utilization of the various macrohabitat types by the four radiotracked Gaboon vipers is presented in Table II.

All the specimens showed a statistically significant preference for the dryland forest clearings (for all specimens, at least $P < 0.00001$ at χ^2 test with $df = 3$). The specimens spent some time even in all the other macrohabitat types available in the study area but not in cultivated land. However, only male B spent considerable time in the swamp forest area. This specimen was never observed swimming or resting in water, but he was frequently observed on the mud and grass surrounding the swamps.

Numerical values of habitat breadth were respectively 2.645 for male A, 2.439 for male B, 1.275 for female C, and 1.1 for female D. These values were

TABLE I

Above-ground activity of four radiotracked Bitis gabonica. The intensity of above-ground activity of each specimen in each daily hour interval is expressed as percent frequency of locations with above-ground active specimen on the total of twenty locations (in twenty different field days, once per day in each daily hour interval). Note that A and B were two males, and C and D were two females.

Day period (hr)	Monitored Specimens			
	A %	B %	C %	D %
0100-0359	10.00	50.00	35.00	60.00
0400-0659	60.00	70.00	75.00	55.00
0700-0959	90.00	90.00	75.00	75.00
1000-1259	5.00	35.00	0	0
1300-1559	0	5.00	5.00	5.00
1600-1859	90.00	30.00	75.00	5.00
1900-2159	90.00	95.00	40.00	50.00
2200-2459	50.00	60.00	5.00	60.00
Above-ground active fixes:				
Total <i>N</i>	89	87	47	62
Total %	55.6	54.4	29.4	38.7

TABLE II

Total number of locations of four radiotracked Bitis gabonica in the various macrohabitat types available in the study area. Note that a total of 160 locations per specimen were performed, and that A and B were two males, and C and D were two females.

Habitat type	Monitored specimens			
	A	B	C	D
Thick dry forest	35	20	13	1
Clearings	88	93	141	152
Grassy area	22	11	3	7
Swamp-forest	15	36	3	0
Cultivated land	0	0	0	0
Total <i>N</i>	160	160	160	160

significantly higher in males than in females (intersexual differences significant at least at $P < 0.0005$, nonparametric correlation matrix Mantel test). This intersexual difference depended on the fact that the two females used almost exclusively the

dry forest clearings (Table II). However, overlap estimates indicated that both males and females were relatively similar in their macrohabitat use frequency (Table III).

TABLE III

Matrix showing the numerical overlaps in terms of macrohabitat similarity between four radiotracked individuals of Bitis gabonica. The matrix values were generated by applying Pianka's (1973) symmetric equation. For more details, see text. Note that A and B were two males, and C and D were two females.

	B	C	D
A	0.639	0.764	0.803
B	****	0.781	0.818
C		****	0.921
D			****

There was not any significant association between day time interval and percent frequency of observations of snakes in a given macrohabitat (MANOVA with the macrohabitat type as the factor, the individual snakes, the various field days and the daily-time-intervals as the covariates: $P > 0.2$). Thus, there was not any apparent pattern for snakes to concentrate in thick forest sites during the hottest hours of the day.

The fact that male vipers had a macrohabitat use breadth higher than females could be correlated with their higher daily movement rates and with their larger home ranges (see below). It is likely that these patterns could be linked to the mating strategies of males, as (i) evidences of occurrence of a mating season were collected during the short period of this research (see below), and (ii) it has been demonstrated that, in viperid snakes, males tend to move more than females to search for a mating opportunity and to mate with multiple females (Madsen *et al.*, 1992, 1993; but see also Capula & Luiselli, 1994; Luiselli, 1995).

The apparent tendency of monitored specimens to avoid cultivated lands confirms previous suggestions by Luiselli & Akani (1998) that Gaboon vipers are very rare in farmlands, plantations, and suburbia. This is important from the snake-*versus*-humans relationships perspective, as it limits the potential for encounters between farmers and vipers, thus reducing the possibility that lethal cases of envenomation could occur. Indeed, it seems that the spitting cobra (*Naja nigricollis*), a venomous species well adapted to life in farmlands and suburbia (Luiselli & Angelici, in press), is responsible of the great majority of the cases of serious envenomations to humans in southern Nigeria (Luiselli *et al.*, research in progress).

ACTIVITY TYPES

Pooling together all the radiotracked animals, we recorded the activity type exhibited by Gaboon vipers on a total of 255 locations, given that in some instances this type of data was not collected. Pooling the four specimens, it resulted that in most cases the vipers were alone and coiled (41.6 % of the total sightings) or alone and partially lying stretched out (40.4 %), whereas they were engaged in locomotion on 10.6 %, in social groups on 4.3 %, and in feeding on 3.1 % of the sightings.

During their locomotory activity, the vipers were almost imperturbable to external stimulus, including tactile and vibrational stimuli. When disturbed, they were reluctant to bite, despite we never tried to provoke intensely their reaction. On six different times, the locomotory activity of Gaboon vipers was accompanied by alarm calls and perturbed movements of small groups of monkeys (*Cercopithecus mona*) climbed on trees adjacent to the places where the snakes were moving.

Starin & Burghardt (1992) also recorded alarm calls of monkeys (*Erythrocebus patas* and *Procolobus badius temminckii*) perturbed by movements of snakes (*Python sebae*). The alarm calls of the monkeys in the presence of viper movements suggest that these arboreal primates recognize these snakes as potential predators. In fact, although we have never recorded any case of monkey-eating by Gaboon vipers during our field studies, nevertheless occasional cases of predation of these vipers upon young monkeys have already been reported in the literature (Spawls & Branch 1997).

Male combats (always between a radiotracked male and another contestant) were observed just twice, once at hr 0740 and once at hr 0936. The fighting vipers did not bite each other, and were not disturbed at all by the presence of human observers. Courtship and copulations were observed nine times, usually in late afternoon (hr 1750 to hr 1945, five cases), but also in the early morning (hr 0535 to hr 0725, three cases) and at midday hours (hr 1315, one case). All the courtship and mating events always occurred inside thick bushes, whereas one of the two male combats occurred in open territory, on a leaf litter substratum. All the social groups observed during this study consisted only of two specimens, and despite our careful monitoring of the space surrounding the interacting animals, no other viper occurred in the vicinity of the two contestants (in case of sexual combat) or of the two partners (in case of sexual interaction). Displays exhibited by Gaboon vipers during mating and combats have already been described elsewhere (Akester, 1979a, 1979b, 1984).

Gaboon vipers were observed on four instances to feed upon striped rats (*Lemniscomys striatus*), and on other four instances upon undetermined rodents. In three of such instances the vipers sat on leaf litter in the swamp forest area, in three cases they were on leaf litter in the dry forest clearings, and in two cases they were on leaf litter in the thick forest area. Six of the eight events occurred in late afternoon (hr 1620 to hr 1950), and two during the night (hr 2305 to hr 0220).

Data collected during this radiotelemetric study confirmed that rodent prey is no doubt the major food source of Nigerian Gaboon vipers, as already suggested by Luiselli *et al.* (1998b). Moreover, the daily distribution of the recorded predation events indicates that much of the Gaboon viper foraging activity is conducted between the late afternoon and the early night hours. It is likely that the viper activity peaks recorded during such hours could be also due to intense foraging activity at this time.

DAILY MOVEMENT RATES AND HOME RANGES

Average daily distances moved were small in females ($x = 23.1$ m, $SD = 26.5$, $n = 20$), and much larger in males ($x = 47.1$ m, $SD = 55.7$, $n = 20$). This intersexual difference was significant ($P < 0.05$, Mann-Whitney U test).

Average distances moved were smaller during the day than during the night in both males (day: $x = 23.7$ m, $n = 20$; night: $x = 71.3$ m, $n = 20$) and females (day: $x = 11.4$ m, $n = 20$; night: $x = 39.6$ m, $n = 20$). This day/night difference was statistically significant in both sexes ($P < 0.005$, Mann-Whitney U test).

Home-ranges averaged 1.6 ha in the males and 0.8 ha in the females. Due to the small sample of examined specimens we did not compare statistically the intersexual home range differences.

The radiotracking study has revealed that daily movement rates are (1) nocturnally higher than diurnally and (2) higher in males than in females. These patterns are consistent with the above-mentioned peaks of above-ground activity observed during night in the radiotracked specimens. The larger home ranges of males are also clearly correlated with the larger male daily movement rates.

GENERAL OBSERVATIONS

Throughout the radiotracking period, we recorded a lot of empirical informations on the activity of the Gaboon viper which, however, are difficult to quantify. In this section, we briefly summarize these observations.

Above-ground activity of Gaboon vipers appeared strongly conditioned by rainfall and humidity level. During the central daylight hours (hr 1000 to hr 1600), we found above-ground active Gaboon vipers during relatively cool days, characterized by alternate showers and sunny periods. During the nocturnal hours (hr 1900 to hr 0600), the viper above-ground activity was intense when the daylight hours were dry and hot. Conversely, when the daylight hours were characterized by showers, it was very difficult to find any above-ground active specimen throughout the nocturnal time.

Our radiotracking procedure permitted to identify the sheltering sites of these vipers in 20 instances. Gaboon vipers sheltered into cavities and holes under piles of wood and inside muddles of roots at the basis of large trees (8 cases), in rodent holes (6 cases), termite nests (5 cases), and even under piles of molluscan shells used as food by people and cumulated in a forest clearing surrounding the village (1 case).

Contrary to European *Vipera* species (Saint Girons, 1975a, 1975b, 1978; Naulleau, 1979, 1983), basking in the open was not a common event. Indeed, the Gaboon vipers preferred to rest with much of the body inside bushes, thus exposing to the open only a small portion of the body. On the other hand, they were found wholly in the open, and even completely motionless, in the shadow, especially during late evening.

CONCLUDING REMARKS

Though based on a little number of specimens our radiotracking study has permitted to address some aspects of the secretive life of these little known tropical forest snakes. However, some limits deserve to be reminded.

To begin with, the comparisons between sexes were based on very small samples, and thus it is possible that some of the observed patterns could be attributable to behavioural variability between individuals rather than between sexes. In any case, this potential limit is shared with a number of other radiotelemetric studies on snakes and other vertebrates, which are also based on the monitoring of very few specimens under the assumption that the radiotracked individuals could be representative of their sex, age class, etc.

In addition, the data were collected entirely during the dry season. This could partially affect our conclusions, as the remarkable differences between wet and dry seasons in the Nigerian climate could translate into important interseasonal behavioural differences by the vipers, which are strongly influenced by seasonality in their biological rhythms (Bodbiel, 1994; Luiselli & Akani, 1998).

Moreover, the timespan of viper monitoring during the present study (20 days) was too short to address any firm conclusion about the sedentarity of these vipers, that could indeed change seasonally as is the case of other viperids studied to date (e.g. see Viitanen, 1967).

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